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Starvation in a field population of litter-inhabiting Collembola Methods for determining food reserves in small arthropods

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With 2 figures

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1. Introduction

Studies on food preferences of Collembola have led to the conclusion that nearly all collembolan species are more or less unspecialized feeders (Petersen 1971, McMillan 1975). Anderson & Healey (1972) considered this food generalisation to be associated with an excess of food. In another view, however, food generalisation. (i.e. a varied diet) might have a selective advantage when particular food becomes rare (Emlen 1973) whereas food specialisation (e.g. selection of food items with relatively rich energy contents), could be stimulated in an excess of food (Schoener 1971).

This controversy gave rise to an investigation of the feeding condition of Collembola in the field (Joosse & Testerink 1977a). In *Orchesella cincta* (L.) occasionally high percentages of animals were found with an empty gut during the summer in periods of drought and during the winter. It was suggested that these high percentages were caused by the absence or inaccessability of food in summer, and too low a temperature in winter when most ectothermic animals do not feed (Van der Drift 1951, Barlow 1957, Gere 1962).

The important question remains whether the empty gut is indicative of starvation. An empty gut can to a certain extent be accounted for by the frequent moults. During the preparation of a moult the animals do not feed for several days (De With & Joosse 1971). Some phenomena suggest that the population structure is sometimes profoundly changed when high frequencies of an empty gut occur. Joosse & Testerink (1977a) observed many individuals with an empty gut during dry periods in several summers and found after this little feeding activity, a change in the age structure of the population of *O. cincta*. This was caused by a sharp increase in the number of newly hatched individuals. When, in laboratory experiments such a lack of feeding was brought about by food deprivation, it was found that starvation led to an arrest of several vital activities such as egg production, moulting and locomotory activity (Joosse & Testerink 1977b). Subsequent feeding resulted in a synchronised reproduction. Thus in the field the phenomenon of an empty gut as a result of starvation could be correlated with important consequences for the individual and the population.

In the present paper the effect starvation has on springtails was studied in the laboratory to determine whether and when an empty gut can be interpreted as starvation. Starvation is defined as a condition in which food reserves i.e. lipids and glycogen are being used up. The amount of food reserves was further used to analyse the feeding conditions of a field population of *O. cincta*. The study lasted for about one year (summer 1976 — spring 1977).

2. Materials and Methods

2.1. Introductory note

The species used in this study, *Orchesella cincta* (L.), lives in the litter of forests. The animals were collected from the litter of a pine plantation (*Pinus sylvestris* L.) near Hilversum, The Netherlands. A sample of these animals was used in the laboratory to analyse the effects of starvation on their food reserves (lipid and glycogen contents). Another sample was used to determine the nutritional condition of animals in the field.

2.2. Laboratory experiments

The animals were kept in PVC jars (⌀ 5 cm) with a layer (2 cm) of moistened plaster of Paris. They were fed with *Pleurococcus* spec. (green algae). After an acclimation period of 1 week at 15 °C, one group of animals was deprived of food, another group was fed continuously. Twice a week the jars were replaced. The light regime was 12 h L and 12 h D. Twice a week samples of starved animals were analysed for lipid and glycogen content. At the end of the experiment the fully-fed control animals were tested. The experiment lasted for 3 weeks.

Total lipids were extracted by using the method of BLIGH & DYER (1959). The lipid content was determined by the sulphophosphovanillin method (BARNES & BLACKSTOCK 1973) using springtail lipids as standards. Per determination 5 individuals were used and every determination was repeated five-fold.

Thy glycogen content was determined by the anthron method (VAN HANDEL 1965) (5×10 animals).

2.3. Field observations

The percentage of animals with gut contents was determined form hand-collected samples. The animals, sieved out of the litter layer were put in fixative at the sampling site by the Gisin's method (1960). After some days they were cleared in 10% KOH and the gut contents, when present, were then easily visible. The samples consisted of at least 200 individuals.

For the determination of lipid and glycogen content animals were transported to the laboratory in PVC jars. The animals were immediately weighed on a Mettler ME 30 micro-balance and temporary stored in a deep-freeze. The analysis was performed as described above. The data for temperature and rainfall data were obtained from the nearest weather station.

3. Results

3.1. Experiments to measure the lipid and glycogen content during starvation in the laboratory

The effect of starvation on lipid and glycogen content of individuals of *O. cincta* is listed in Table 1. The results show that the lipid content, initially about 15% of the dry weight, remained constant during the first 3 days of starvation. On the 7th day it appeared to have decreased and afterwards remained at a level of about 10% of the dry weight. The glycogen content, initially about 1% of the dry weight, decreased within 3 days to about zero.

The conclusion can be drawn that starvation leads to the using up of food reserves, first glycogen and afterwards lipids. These values are further used as standards to show whether an empty gut in field animals is indicative of starvation.

Table 1. The effect of starvation on the lipid and glycogen content (± S.E.) of *O. cincta* at 15 °C in % dry weight

		% lipids	% glyocgen
days starvation	0	*14.9 ± 0.7* a	*1.0 ± 0.2* a
	3	*14.3 ± 1.0* a	*0.1 ± 0.1* b
	7	*10.5 ± 0.9* b	*0.1 ± 0.1* b
	10	*10.6 ± 0.8* b	*0.1 ± 0.1* b
	14	*9.7 ± 0.6* b	*0.1 ± 0.1* b
	21	*10.3 ± 0.4* b	*0.1 ± 0.1* b
fed with *Pleurococcus* spec.	21	16.6 ± 0.6 a	0.9 ± 0.1 a

Groups sharing a common letter do not differ significantly ($p > 0.05$, WILCOXON-test).

3.2. Nutritional conditions of a population in the field

The nutritional conditions of *O. cincta* in the field has been determined by measuring the lipid and glycogen content during the summer of 1976, the following winter and early spring of 1977. The summer data are presented in Figure 1 and are compared with the prevailing

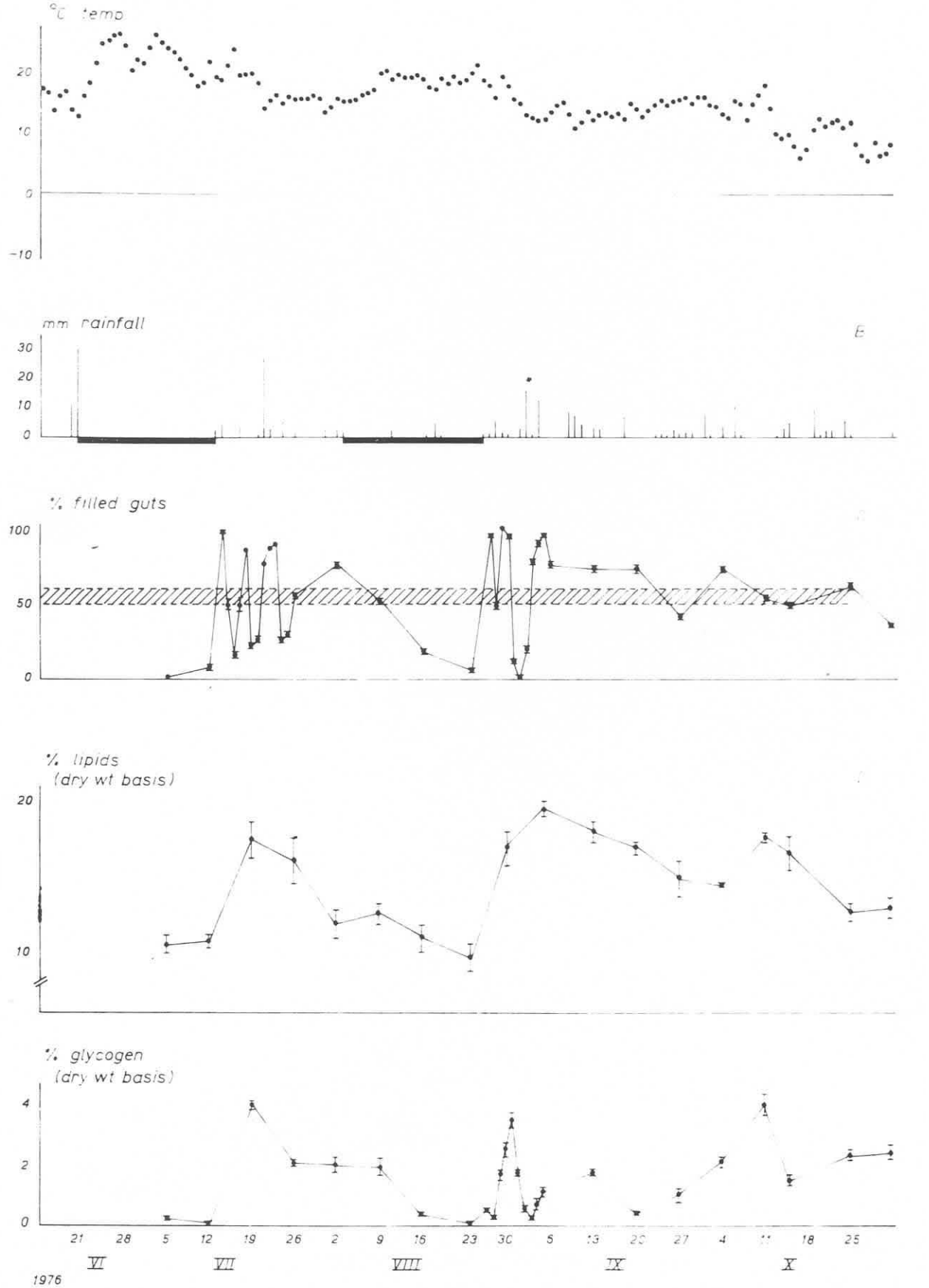

Fig. 1. Percentages of animals with gut contents (C), the percentage of lipids (D) and the percentage of glycogen (E) (± S.E.). The investigated dry periods are indicated below the abscissa of the rainfall diagram (B). The shaded area in c indicates the expected percentage of animals with gut contents at temperatures (a) above 10 °C.

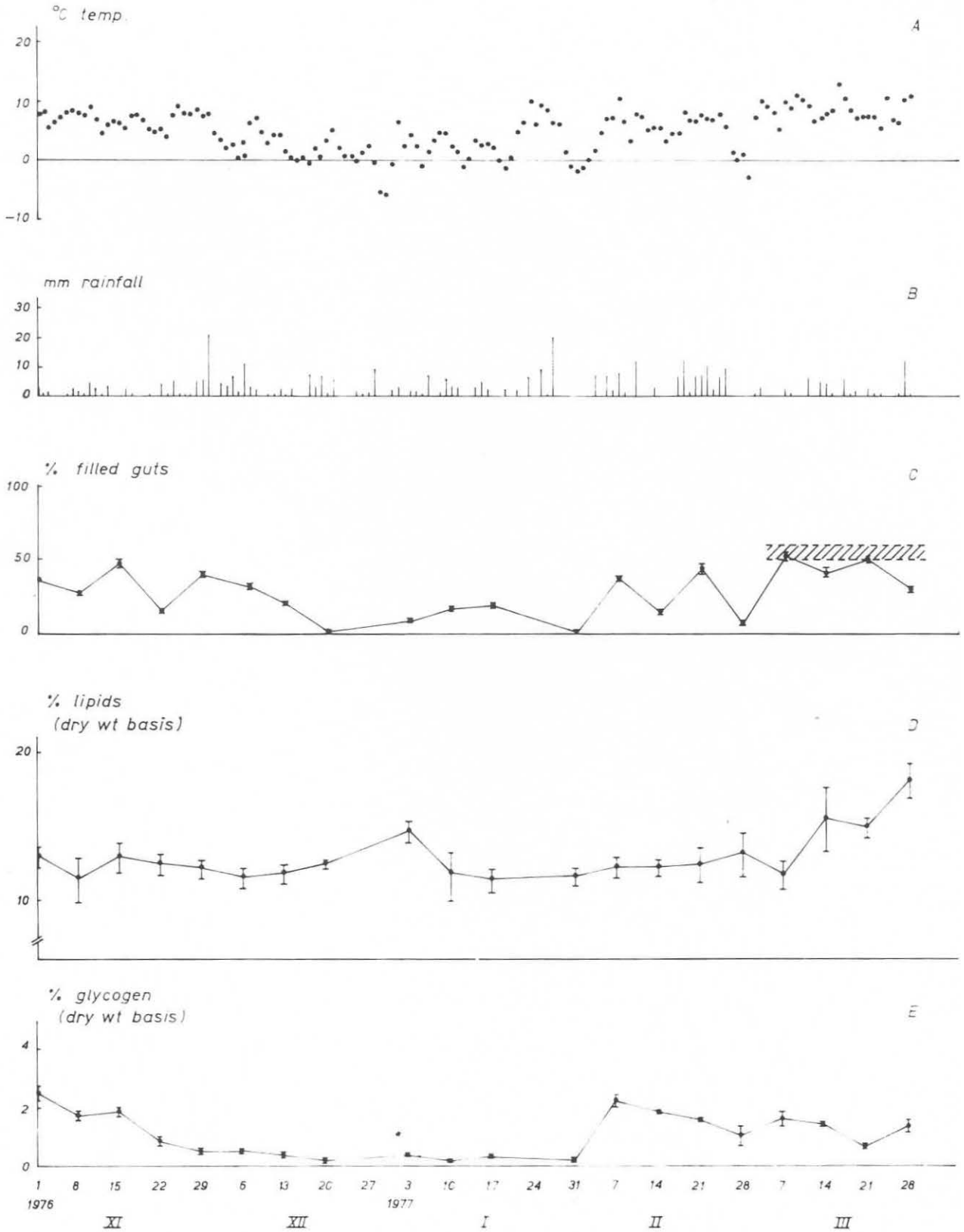

Fig. 2. Percentage of animals with gut contents (C), the percentage of lipids (D) and the percentage of glycogen (E) (± S.E.). The shaded area in c indicates the expected percentage of animals with gut contents at temperatures (A) above 10 °C.

temperature and rainfall (Figure 1A and 1B). The results show that the percentage of animals with gut contents (Figure 1C) fluctuate widely. This is partly related to moulting phenomena, since moulting animals do not feed for several days. Observations in the laboratory made clear that as a result the average percentage of animals with gut contents was expected to be 50 to 60%, at least at temperatures above 10 °C (JOOSSE & TESTERINK 1977a). This range is indicated in Figure 1C.

It can be seen that many deviating data have been recorded. Very low percentages of animals with gut contents were found during dry periods of June—July and end July—August. From data on the food reserves of the animals during these periods, as presented in Figure 1D (lipids) and 1E (glycogen), it can be seen that these data correspond with a decreased content of lipids (about 10% of the dry weight) and glycogen (about 0% of the dry weight). As shown above this can be interpreted as starvation.

After the dry periods a synchronisation of feeding activity and moulting occurred, recognizable from an alteration in the ratio of filled to empty guts (JOOSSE & TESTERINK 1977a). The percentage of lipids increased during this synchronization to about 18% of the dry weight. During a moulting interval the lipid content does not fluctuate greatly (TESTERINK in prep.). The percentage of glycogen increased within a few days to about 4% of the dry weight. The daily measurements at the end of August and early September demonstrate that the glycogen content fluctuated during synchronization between about 4% and 0% of the dry weight.

The conclusion can now be drawn that an empty gut does not necessarily indicate starvation. Measurements of the food reserves are necessary for determination of starvation. It is concluded that *O. cincta* starved during the dry periods in summer.

The winter data on the nutritional conditions of the *O. cincta* population are presented in Figure 2. Very low frequencies of animals with gut contents could be found during December—February. The lipid content (Figure 2C) decreased to about 12% of the dry weight and the glycogen content decreased to about 0.3% of the dry weight. This means that during the winter the animals do not feed and consume their food reserves, that is they are starving.

January 3rd was an interesting date when after a sharp increase in temperature a significantly ($p < 0.05$, WILCOXON-test) high lipid content was found indicating a building up of the food reserves, comparable to the situation in spring. The larger fluctuations in the percentage of animals with gut contents (Figure 2C) suggest again a synchronized feeding and moulting activity.

4. Discussion

Starvation in field populations of decomposers has been demonstrated very seldom (REMMERT 1978). For a population of Collembola starvation appeared to be a rather frequent and very important phenomenon, for during starvation reproduction is arrested, resulting in important effects for the population structure and numbers. The present study showed that for a characterization of starvation in small arthropods in the field, a simple determination of the occurrence of an empty gut is inadequate. A more suitable parameter for starvation is found to be the amount of food reserves, i.e. lipids and glycogen, for during starvation these food reserves are used up. The method introduced here can be applied in field studies of very small animals.

By using this method it can be demonstrated that *O. cincta* under natural conditions starved during dry periods. JOOSSE & TESTERINK (1977a) dicussed the possibility that starvation during dry periods is caused by an absence or inaccessability of food by drying out of the habitat. However, found in larvae of *Tenebrio molitor* L. [MURRAY 1968], starvation during dry periods may also be the result of an arrest of feeding activity, although food is present. Possibly under dry circumstances also in Collembola the feeding activity and consequently the moulting activity is arrested. Such an arrest of the feeding-moulting rhythm during starvation could be of survival value since ecdysis is correlated with high transpiration rates (VERHOEF 1978). Moreover VANNIER & VERHOEF (1978) demonstrated for *Orchesella villosa*

(Geof.) that gut contents might be disadvantegeous because the transpiration rate in fed animals is higher than in starved ones. At any rate under dry circumstances *O. cincta* showed the ability to survive dry periods (Verhoef & Van Selm 1978).

During winter low reserves of lipids and glycogen and a very high percentage of animals with an empty gut indicate starvation. As a result, growth is arrested (Joosse 1969, Joosse & Veltkamp 1970). This effect of low temperature on the feeding activities of soil arthropods is widespread and described by Van der Drift (1951), Barlow (1957) and Gere (1962). Sømme & Conradi-Larsen (1977) analysed the significance of an empty gut in *Tetracanthella wahlgreni* Linnaniemi and found that feeding stops during autumn and that the gut of the animals is gradually emptied. In this species and in several other species like the Collembola *Cryptopygus antarcticus* Willem [Block et al. 1978], *Isotomurus alticola* (Carl) and *Isotoma viridis* Bourlet [Block & Zettel 1980] and the mites *Alaskozetes antarcticus* (Michael) [Block et al. 1978], *Calyptoretes sarekensis* (Träg.) and *Carabodes labyrinthicus* (Mich.) [Sømme & Conradi-Larsen 1977] an interesting correlation between gut contents and supercooling was demonstrated. According to Salt (1966) the empty gut can be considered of survival value since food particles are very efficient nucleating agents and, when present during low temperatures, rob insects of supercooling potentials.

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6. Summary • Zusammenfassung

The occurrence and the effects of starvation in a population of *Orchesella cincta* (L.) has been studied in the laboratory and in the field. In the laboratory the effects of food deprivation on the food reserves, i.e. lipids and glycogen was determined. The lipid and glycogen content decreased to a stationary level. The values have been used as a standard in studying the nutritional condition of *O. cincta* in the field. Under natural conditions starvation occurs during dry periods in summer and during low temperatures in winter. It is suggested that an arrested feeding activity in summer results in a lower transpiration rate and in winter is related to a lowering of the supercooling point.

Hunger in einer Freilandpopulation laubstreubewohnender Collembolen Methoden für die Bestimmung der Nährstoffreserven in Kleinarthropoden

Die Existenz und die Effekte von Hunger wurden an einer Laboratoriums- und einer Freilandpopulation von *Orchesella cincta* (L.) untersucht. Im Laboratorium wurden die Hungereffekte an Hand des Gehaltes an Lipiden und Kohlenhydraten bestimmt. Der Gehalt an Lipiden und Kohlenhydraten nahm bei Hunger bis auf ein konstantes Niveau ab. Diese gefundenen Werte wurden als Standard für die Analysen über den Ernährungszustand von *O. cincta* in der freien Natur gebraucht. In der freien Natur hungern die Tiere während Trockenperioden im Sommer und Kälteperioden im Winter. Es wird vermutet, daß eine stagnierte Ernährungsaktivität im Sommer mit einer erniedrigten Transpiration und im Winter mit einer Erniedrigung des Unterkühlungspunktes korreliert ist.

7. Literature

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